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(Article begins on next page)

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Osteology, fossil record and palaeodiversity of the European lizards

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Abstract. The capability of palaeontologists to identify fossil remains of a particular group of vertebrates strongly depends on the knowledge they have of its comparative osteology and on the actual presence of diagnostic differences among the considered taxa. This could have a relevant influence on the study of palaeodiversity, since a low recognisability causes a loss of data when trying to reconstruct the history of taxa that lived on Earth in the past. Currently, more than 6000 extant species of lizards and worm lizards are known, and new ones continue to be discovered, mainly based on molecular data. But are we able to recognise this high diversity using osteology? As far as European taxa are concerned, the osteological recognisability of non-snake squamates is very low: only 31% of the extant European taxa can be identified based on their skeletal morphology. This is balanced partially by the fact that most recognisable taxa have been actually recognised in the fossil record, suggesting that the lost data are mainly due to the scarce knowledge of the comparative osteology of these reptiles and less influenced by other biases, such as taphonomic or collection biases. In this context, specimen-level phylogenetic analysis has proved to be a useful tool to identify diagnostic combinations of osteological features, at least for lacertid species, as evidenced by a case study focused on the genus *Lacerta*.

Keywords: Identification, Squamates, Reptiles, Palaeontology, Biodiversity

Introduction

Non-snake squamates (i.e., lizards and worm lizards) exist since at least the Middle Jurassic (Rage, 2013), and are represented by more than 6000 extant species worldwide (Uetz and Hošek, 2016) and a number of extinct taxa (for a summary of extinct species see the now dated review of Estes, 1983, but also Böhme and Ilg, 2003). In order to identify the current diversity of these reptiles, herpetologists can rely on various different tools, in particular external morphology, behaviour, molecular and distributional data. Lately, the rate of new lizard descriptions was rising considerably

(Pincheira-Donoso et al., 2013). But what about the palaeodiversity? How precisely can we recognise the diversity of taxa that lived on Earth in the past? Except for a few remarkable examples (e.g., specimens in amber that preserve also the integument like *Succinilacerta succinea* (Boulenger, 1917) or those recently described by Daza et al., 2016), vertebrate palaeontologists are mostly restricted to osteological features to identify fossil remains and study palaeodiversity. This makes the task of palaeoherpetologists much more complex and error-prone than that of neoherpetologists, given that it strongly depends on the degree of knowledge of the comparative osteology of the considered group and on the actual presence of diagnostic differences among the taxa. We here try to quantify the current osteological recognisability of the extant European non-snake squamates, in order to evaluate to what degree it affects our ability to comprehend the past diversity of these reptiles in the continent. The degree of recognisability is also evaluated at different hierarchical levels and within different clades, in order to understand where the information is scarcer and new studies are needed. Last but not least, we try to assess the utility of phylogenetic analyses to identify diagnostic osteological features for lizards, and lacertids in particular.

Materials and methods

We included 75 species of lizards and 3 worm lizards in our analysis. The included species correspond to the European amphibians and reptiles reported by Sillero et al. (2014), plus the lizards and worm lizards living on the Greek islands along the coast of Asiatic Turkey as reported by Speybroeck et al. (2016). Recently introduced taxa have been excluded (as e.g., *Chamaeleo africanus*). The definition of Europe largely follows Arnold and Ovenden (2002), but with the exclusion of Madeira and the Canary islands in the west, because they do not belong to the continent in geological terms.

The evaluation of the recognisability of the different taxa is based on existing bibliography, as well as on personal observations (see supplementary text S1 for a list of the studied specimens). Details about the osteology of European lizards and worm lizards have been mentioned in more than 90 papers,

either dealing directly with comparative osteology (e.g., Evans, 2008) or simply reporting features in the remarks of the identification of fossil material of extant taxa (e.g., Blain, 2009). For a complete list of these works, see supplementary text S2. In order to avoid circular reasoning (as outlined by Bell et al., 2010), geographical and/or chronological criteria are not considered useful for the identification of a taxon, since the range of a species may strongly vary during time.

The recognisable taxa are not always represented by species, but often by different kinds of higher taxonomic ranks. Because of this, the recognisability is here analysed in two ways: 1) in terms of Operational Taxonomic Units (OTUs), regardless whether they represent family, genus or species level; and 2) at the level of species, genus, and family separately. The first analysis tells us how many taxonomic bins can be recognised when having skeletons of all the 78 extant European lizards, in order to depict the recognisable diversity based only on osteology. This diversity is then compared with the actual one recognised by neoherpetologists using other tools, in which OTUs are represented by the 78 extant species of European lizards and worm lizards. The second analysis quantifies how many species, genera, and families of lizards can actually be diagnosed with osteological characters, and, assuming that diagnostic characters are present, in which taxon we need more work to be done to increase this recognisability. Finally, given the widespread individual variation in lizard skeletons, and thus the low probability to find unambiguous, osteological autapomorphies for the species, we implemented a case study to evaluate the utility of specimen-level phylogenetic analysis for the identification of diagnostic combinations of osteological features of the European species of the genus *Lacerta* (as defined by Arnold et al., 2007). We compiled a novel phylogenetic matrix based on osteology only, including 159 character statements taken from earlier works (see references in the supplementary text S2) and personal observations of ET. These character statements were scored in 37 OTUs consisting of single specimens (see supplementary text S1), which were identified before skeletonization, based on external morphology by the collectors or curators of the respective collections. The matrix was compiled in the software Mesquite v. 3.04 (Maddison and Maddison, 2015), and includes nine specimens of *Lacerta agilis*, nine specimens of *Lacerta bilineata*, five specimens of *Lacerta schreiberi*, four specimens of *Lacerta trilineata*, and four specimens of *Lacerta viridis*, which have all been scored based on first hand observations. The outgroup consists of specimens of the European lacertids *Timon lepidus* (1), *Podarcis muralis* (2), *Archaeolacerta bedriagae* (1), *Algyroides nigropunctatus* (1), and *Psammodromus algirus* (1). The matrix was analysed with TNT v.1.1 (Goloboff et al., 2008). We used an extended implied weighting approach (Goloboff, 2014) in order to reduce the influence of highly variable characters and

missing data. The tree search was performed using the New Technology Search, enabling all algorithms, and stabilizing the consensus tree five times with a factor of 75. In order to find all most parsimonious trees (MPTs), a second iteration of tree bisection and reconnection was performed.

Results

Recognisability

The recognisability of European lizards and worm lizards appears to be rather low (Tab. 1): the recognisable OTUs represent only 31% (24 out of 78 taxa) of the current European lizard diversity. A large number of lacertids and scincids, as well as all species of the genus *Anguis*, can only be identified at genus or even at family level (species complex in the case of *Anguis*). It has to be noted that agamids and chamaeleonids are poorly identifiable too, but since a single autochthonous species of each family is currently present in the continent, this has no evident effect on the count of the recognisability of extant taxa. Finally, the most recognisable group is Gekkota: all four species, belonging to four different genera, are clearly distinguishable from one another.

The second analysis shows that recognisability highly depends on the hierarchical levels. Whereas all families of lizards are recognisable based on osteological features, only 45% of the genera and 17% of the extant species are known to have diagnostic features in their skeletons (Fig. 1). Also the degree of recognisability varies greatly within the different families: nearly half (43%) of the scincid and lacertid species can only be identified as belonging to Scincidae and Lacertidae, and the two European species of agamids and chamaeleonids cannot be distinguished from other, non-European members of their family based on osteology. On the other hand, osteological characters of the anguids and blanids allow to recognise all European taxa at least at the genus level (Fig. 2).

As for the European fossil record, a large number of the recognisable OTUs have been identified (20 out of 24, 83%; 26% of the 78 extant species, meaning a loss of data of 74%; Tab. 1). Among the 24 OTUs, in fact, only those corresponding to *Euleptes europaea*, *Mediodactylus kotschyi*, *Lacerta schreiberi* and worm lizards of the *Blanus strauchi* complex have never been recovered as fossils.

Phylogenetic analysis

The first run of the case study of *Lacerta* produced a single MPT of a length of 39.25405, and recovered the specimen of *T. lepidus* among the specimens of *Lacerta*. Given that all the recent phylogenetic analyses including these two genera find them as sister taxa (e.g., Carranza et al., 2004; Arnold et al., 2007; Kapli et al., 2011; Mendes et al., 2016), our result indicates that either we did not find enough osteological characters to unite *Lacerta* to the exclusion of *Timon*, or that the osteological variability is too high to obtain a meaningful tree topology based on osteological characters only. In order to test this, we performed a second analysis, including a constraint forcing the software to find all the specimens of *Lacerta* as a monophyletic group. This second run resulted in nine MPTs with a length of 39.80892. With the exclusion of a single specimen of *L. viridis*, all the other specimens form monophyletic clades with their respective species members in the strict consensus tree (Fig. 3).

Discussion

The impact of recognisability on the study of fossil European non-snake squamates

The knowledge we have of past ecosystems is incomplete, because of the different biases that cause loss of information in the palaeontological record (among others, Dunhill et al., 2012). Among them, taphonomic bias has a major effect, in particular when it comes to small animals (Soligo and Andrews, 2005; Cooper et al., 2006). When an excavation is not directly focused on the recovery of small vertebrate remains, a collection bias may also occur, caused by the difficulty of discovering and collecting

small bones without proper methods and tools. This latter issue is particularly significant when old works are considered, whereas an increased attention towards these fossils became established in XX century. Finally, also a historical bias probably influenced the fossil record of poorly studied vertebrates, such as lizards: studies on their osteology were, in fact, rare until about the 1970s, with a significant increase from the 1980s onwards (Fig. 4). This increase in the number of lizard osteology papers still continues: nearly 25% of all the descriptions used for the current study were published between 2010 and 2016. Obviously, this lack of osteological data until recently hampered the identification of fossil taxa, even if the increasing number of description is highly promising for the future. Also, current taxonomic trends based on molecular analyses tend to raise subgenera and subspecies to genus and species level, respectively (e.g., Arribas and Carranza, 2004; Arnold et al., 2007), and it remains to be seen if this is also reflected in their osteology.

The mentioned biases result in a significant loss of data, especially in small, fossil vertebrate taxa whose comparative osteology is poorly known, such as amphibians or reptiles. Delfino (2004) estimated the loss to be of 58% when comparing the Italian palaeoherpetological fossil record with the extant Italian herpetofauna. Within lizards, only the 36% of the diversity of extant Italian species has been recognised in the fossil record (Delfino, 2004), which amounts to a loss of data of 64%.

Results are even worse when fossils of all European lizards and worm lizards are considered, with an increase in the lost information of 10% (74% versus the above-mentioned 64% in Italy). The same holds true for the percentage of recognisability of extant lizards, which is 44% for Italian species (Delfino, 2004) and only 31% for European ones. The trend of decreasing recognisability when going from higher to lower taxonomic levels (Fig. 1) clearly shows that detailed osteological studies are strongly needed at genus and species level. As far as lacertids are concerned, this issue

is exacerbated by the fact that they are the most speciose family of lizards in Europe (56 species out of 78, 72%) and that, among them, the sole genus *Podarcis* includes 21 species, which can currently not be distinguished based on osteology. Moreover, the recognisability of *Podarcis* itself can be also questioned, because of the poor knowledge of the osteology of other small-sized European lacertids that can be potentially confused with it. Nonetheless, as will be shown below, detailed osteological study combined with novel methodological approaches like specimen-level phylogenetic analysis appears to be well suited to identify diagnostic combinations of osteological traits for lacertid species. This promising result indicates that at least for lacertids, if not for all lizards, the main issue decreasing recognisability may not be the lack of osteological traits in their skeletons, but the lack of our current osteological knowledge. As for anguids, this may hold true for the genus *Anguis* too, whose species have been mostly erected based on molecular data (Gvoždík et al., 2010, 2013), and for which no comparative osteological study has yet been published. Finally, despite not distinctly affecting the recognisability of extant European lizards, the fact that both European agamids and chamaeleonids can only be recognised at the family level will likely cause a loss in our knowledge of the past diversity of these two groups because of the absence of characters useful for distinguishing them from extant taxa that are currently extralimital, or from other species that have become extinct in the meantime.

The degree of lost data about the palaeodiversity of non-snake squamates in Europe, at least when extant taxa are considered, is therefore very high, and most probably even higher considering that our estimation is made under the implied premise of an equal probability of fossilization for all taxa. However, as already stated by Delfino (2004), this is probably not true: some taxa (such as *Iberolacerta* spp.) live in environments that complicate fossilization, such as high-altitude forests or areas with acid soils, and nearly no sedimentation. Therefore, these species have lower

probabilities of being preserved in the fossil record. Moreover, some osteological features of certain species (e.g., the scarce robustness of the bones of small gekkotans and scincids) could prevent their preservation. It is also true that fossils are often represented by isolated skeletal elements or incomplete specimens, missing the necessary bones or bone features to identify them. Therefore, even if a species is theoretically recognisable based on its osteology, taphonomic bias often prevents identification of the fossils. Nonetheless, both in the Italian and the European fossil record, most recognisable OTUs have been recovered as fossils (Tab. 1). This further corroborates that the loss of diversity is not significantly due to an absence of remains (i.e., taphonomic and collection biases may be less influent), but mainly due to the lack of detailed knowledge of potentially diagnostic, osteological features.

Given that, it appears evident that an improvement of our knowledge of the comparative osteology of lizards and worm lizards (but also of other reptiles and amphibians) is crucial in order to increase our understanding of the past diversity of these animals (as already pointed out by Bell and Mead, 2014). In particular, agamids, chamaeleonids, lacertids, scincids and *Anguis* need further investigations. The paucity of scholars interested in the comparative osteology of lizards in past times has surely prevented us to have a better capability to recognise fossil representatives of these animals, also because few researchers could not cover the whole extent of lizard diversity. New studies dealing with the osteology of extant species will surely benefit palaeontologists working with Pleistocene and Holocene fossils, which appear to be mostly attributable to modern taxa, but they will have an impact on the study of older fossils as well, because they will allow researchers to better recognise extinct forms and their relationships. Moreover, a better knowledge of the comparative osteology of extant species could also be useful for neoherpetologists to better understand the relationships between them, adding to other information such as external morphology and molecular

data, as shown by our phylogenetic analysis. Finally, only apomorphy-based identifications of fossil and sub-fossil material will allow to overcome the circular reasoning in palaeobiogeographical reconstructions, which led to the flawed recognition of herpetofaunal stability throughout the Pleistocene and Holocene of North American taxa (Bell et al. 2010). We should therefore be cautious with referrals of European Quaternary remains to extant taxa.

The case of Lacerta

Although the high variability within *Lacerta* species was confirmed by our phylogenetic analysis, the second run of the phylogenetic analysis with the constrained searches shows that specimen-level phylogeny can be a useful tool to identify diagnostic combinations of osteological features for lizard species. Given that the vast majority of specimens formed monophyletic clades with the other specimens of the same species, the set of character states uniting these monophyletic clades can be interpreted to be a diagnostic combination of osteological features of the respective species. It is important to stress that most single features of these diagnostic combinations can be variable within a clade, or shared with specimens of other species, so that they can rarely be considered unique autapomorphies of a particular species. However, the combination of all these osteological features is unique, and can be added to differential, morphological diagnoses of the species. The single specimen of *L. viridis*, which was found within the clade formed by the specimens of *L. bilineata*, is very incomplete, and does not preserve cranial material. It is possible that the erroneous placement of this specimen is due to that lack of cranial material, which is generally considered to be more diagnostic at species level than postcranial bones. Also, *L. bilineata* has only relatively recently been separated as distinct species from *L. viridis* (Rykena, 1991; Amann et al., 1997; Marzahn et al., 2016), and no morphological characters have been reported to date to distinguish the two species. Our results therefore appear to corroborate the general

assumption that cranial material is more readily identifiable to the species level than postcranial bones. Finally, it is important to note that only a constrained search managed to find the specimens of a single species in monophyletic clades. This result indicates that in the case of *Lacerta*, osteological characters alone do not seem to be enough to recover a reliable tree topology at the species level. Although the referral of the specimens to a single species was successful in nearly all cases (actually all the specimens that included cranial elements), the position of the *Lacerta* species as found in our strict consensus tree might thus not represent true phylogenetic relationships. More methodological work will be needed to address this discrepancy, but this would be out of the scope of the present study. In any case, the current analysis highlights the utility of specimen-level phylogeny to identify diagnostic combinations of osteological features for lacertid species. It also shows that lizard skeletons bear taxonomically significant features, and that detailed osteological studies are promising for the recognition of diagnostic traits and finally for identifying lizard remains in the fossil record.

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388 **Table 1)** Recognisability of European lizards and worm lizards and their presence in the
 389 fossil record.

Extant species	Recognisable OTU	Fossil record
<i>Laudakia stellio</i>	Agamidae indet.	Yes
<i>Chamaeleo chamaeleon</i>	Chamaeleonidae indet.	Yes
<i>Euleptes europaea</i>	<i>E. europaea</i>	No
<i>Hemidactylus turcicus</i>	<i>H. turcicus</i>	Yes
<i>Mediodactylus kotschy</i>	<i>M. kotschy</i>	No
<i>Tarentola mauritanica</i>	<i>T. mauritanica</i>	Yes
<i>Acanthodactylus erythrurus</i>	<i>A. erythrurus</i>	Yes
<i>Algyroides fitzingeri</i>	Lacertidae indet.	Yes
<i>Algyroides marchi</i>		
<i>Algyroides moreoticus</i>		
<i>Algyroides nigropunctatus</i>		
<i>Anatololacerta anatolica</i>		
<i>Anatololacerta pelasgiana</i>		
<i>Archaeolacerta bedriagae</i>		
<i>Dalmatolacerta oxycephala</i>		

Darevskia armeniaca

Darevskia lindholmi

Darevskia praticola

Darevskia saxicola

Dinarolacerta

montenegrina

Dinarolacerta

mosorensis

Hellenolacerta graeca

Iberolacerta aranica

Iberolacerta aurelio

Iberolacerta bonnali

Iberolacerta cyreni

Iberolacerta galani

Iberolacerta horvathi

Iberolacerta

martinezricai

Iberolacerta monticola

Zootoca vivipara

<i>Eremias arguta</i>	Eremiadini indet.	Yes
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Ophisops elegans

<i>Lacerta agilis</i>	<i>L. agilis</i>	Yes
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<i>Lacerta bilineata</i>	<i>L. bilineata</i>	Yes
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<i>Lacerta viridis</i>	<i>L. viridis</i>	Yes
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<i>Lacerta schreiberi</i>	<i>L. schreiberi</i>	No
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<i>Lacerta trilineata</i>	<i>L. trilineata</i>	Yes
<i>Podarcis bocagei</i>	<i>Podarcis</i> sp. (?)	Yes
<i>Podarcis carbonelli</i>		
<i>Podarcis cretensis</i>		
<i>Podarcis erhardii</i>		
<i>Podarcis filfolensis</i>		
<i>Podarcis gaigeae</i>		
<i>Podarcis hispanicus</i>		
<i>Podarcis levendis</i>		
<i>Podarcis lilfordi</i>		
<i>Podarcis liolepis</i>		
<i>Podarcis melisellensis</i>		
<i>Podarcis milensis</i>		
<i>Podarcis muralis</i>		
<i>Podarcis</i>		
<i>peloponnesiacus</i>		
<i>Podarcis pityusensis</i>		
<i>Podarcis raffonei</i>		
<i>Podarcis siculus</i>		
<i>Podarcis tauricus</i>		
<i>Podarcis tiliguerta</i>		
<i>Podarcis vaucheri</i>		
<i>Podarcis waglerianus</i>		
<i>Psammodromus algirus</i>	<i>Psammodromus</i> sp.	Yes

<i>Psammodromus</i>		
<i>hispanicus</i>		
<i>Timon lepidus</i>	<i>T. lepidus</i>	Yes
<i>Ablepharus kitaibelii</i>	Scincidae indet.	Yes
<i>Ophiomorus</i>		
<i>punctatissimus</i>		
<i>Trachylepis aurata</i>		
<i>Chalcides bedriagai</i>	<i>Chalcides</i> sp.	Yes
<i>Chalcides chalcides</i>		
<i>Chalcides striatus</i>		
<i>Chalcides ocellatus</i>	<i>C. ocellatus</i>	Yes
<i>Anguis cephallonica</i>	<i>Anguis</i> gr. <i>A.</i> <i>fragilis</i>	Yes
<i>Anguis colchica</i>		
<i>Anguis fragilis</i>		
<i>Anguis graeca</i>		
<i>Anguis veronensis</i>		
<i>Pseudopus apodus</i>	<i>P. apodus</i>	Yes
<i>Blanus cinereus</i>	<i>Blanus</i> sp. (Western Group)	Yes
<i>Blanus mariae</i>		
<i>Blanus strauchi</i>	<i>B. strauchi</i> complex	No
78	24 (31%)	20 (26%)

Figure 1) Recognisability of extant European lizards at family, genus and species levels. Numbers inside the columns represent the exact percentage of recognisable taxa and their number compared to the total number of family, genera and species respectively (between parentheses).

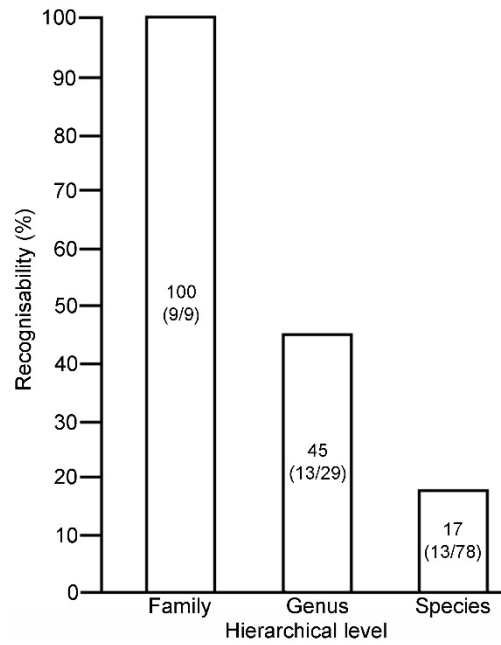


Figure 2) Hierarchical level of the recognisability in the different families of European lizards and worm lizards: percentage of extant species recognisable at family level is depicted in black, percentage at genus level in dark grey, percentage at species level in white, percentage at subfamily or species complex level in light grey. Numbers inside the columns represent the exact percentage of extant species recognisable at a specific level and their number compared to the total number of species included in the family (between parentheses). Abbreviations: Ag, Agamidae; Ch, Chamaeleonidae; Sp, Sphaerodactylidae; Ge, Gekkonidae; Ph, Phyllodactylidae; La, Lacertidae; Sc, Scincidae; An, Anguidae; Bl, Blanidae.

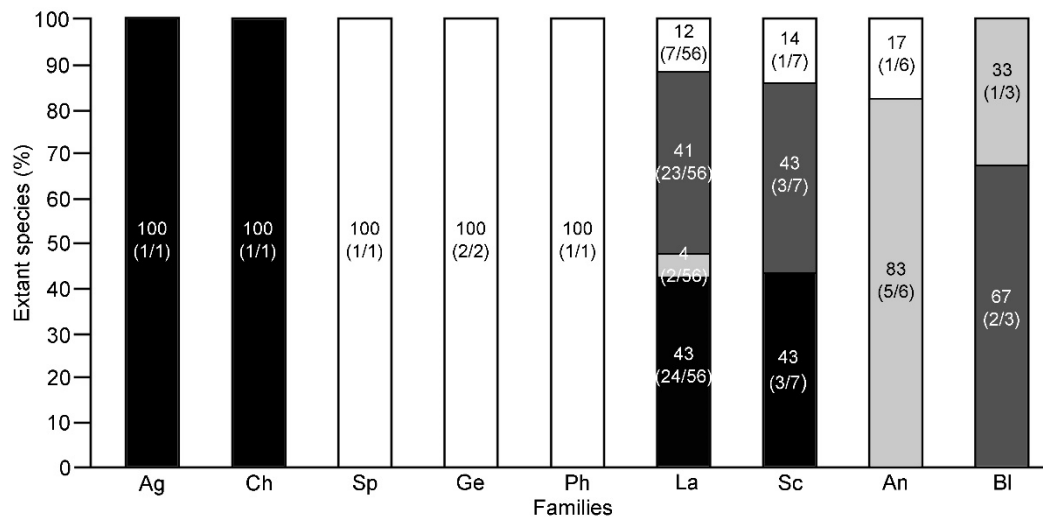
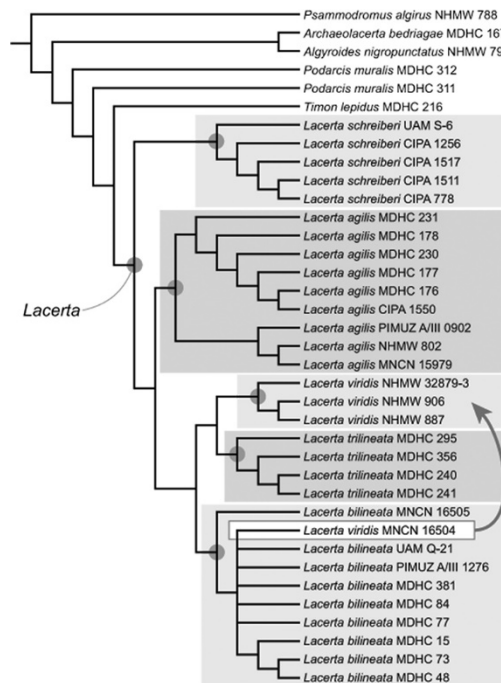
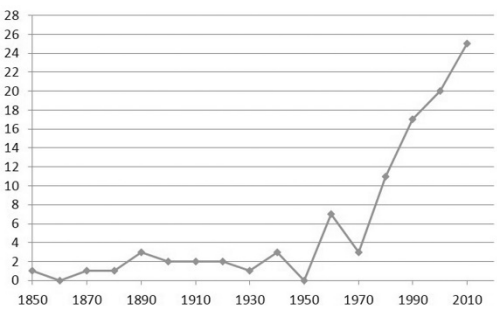


Figure 3) Strict consensus tree of 9 MPTs resulting from a constrained search forcing all specimens of *Lacerta* into a monophyletic clade (as confirmed by phylogenetic studies based on molecular data). All but one specimen (*L. viridis* MNCN 16504, marked in white) were recovered in monophyletic clades together with the other members of their species (highlighted by the grey rectangles). The character states uniting these clades at their base (indicated by dark grey dots) can be interpreted as autapomorphic combination of osteological traits of the respective species, and used to identify fossil material. The questionable position of MNCN 16504 is probably due to the lack of cranial material (the specimen only preserves a partial vertebral column).



419 **Figure 4)** Number of articles dealing with European lizard osteology per 10 years from
420 the 1850s to today.

421



Osteology, fossil record and palaeodiversity of the European lizards

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Supplementary material

Supplementary text S1

List of studied specimens. The specimens marked with an asterisk were included in the phylogenetic analysis. Abbreviations: CIPA - Laboratório Arqueociências Lisboa, Portugal; HUI.OST - Osteological collection of the Hebrew University of Jerusalem, Israel; MCCI - Museo Civico di storia naturale di Carmagnola, Italy; MDHC - Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of Torino, Italy; MNCN - Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN - Muséum national d'Histoire naturelle, Paris, France; NHMW - Naturhistorisches Museum Wien, Austria; PIMUZ - Paläontologisches Institut und Museum der Universität Zürich, Switzerland; UAM.R - Universidad Autónoma de Madrid (Reptiles), Spain; ZMS - Zoologische Staatssammlung München, Germany.

Laudakia stellio: MDHC 245; HUI.OST-Z-5, 423, 424.

Chamaeleo chamaeleon: MNHN 241, 1942-103, 2002-24, 1887-875; HUI.OST-Z-380, 425.

Euleptes europaea: MDHC 384, 388, 389.

Hemidactylus turcicus: MDHC 26, 238

Mediodactylus kotschy: MDHC 201, 285.

Tarentola mauritanica: MDHC 97, 98, 119, 194, 302.

Acanthodactylus erythrurus: UAM.R.AC VII; EBD 1266 (specimen from the collection of Salvador Bailon).

Algyroides fitzingeri: MDHC 351.

Algyroides moreoticus: MDHC 174.

Algyroides nigropunctatus: MDHC 171, 242, 243; NHMW 797*.

Archaeolacerta bedriagae: MDHC 167*; unnumbered specimen from the collection of Salvador Bailon.

Eremias arguta: MNHN 1944-168.

Iberolacerta bonnali: UAM.R.Lm28A.

Iberolacerta cyreni: UAM.R.Lm4.

Iberolacerta monticola: UAM.R.Lm77, Lm92.

Lacerta agilis: CIPA 1550*; MDHC 176*, 177*, 178*, 230*, 231*; MNCN 15979*; NHMW 802*; PIMUZ A/III 0902*.

Lacerta bilineata: MDHC 15*, 48*, 73*, 77*, 84*, 381*; MNCN 16505*; PIMUZ A/III 1276*; UAM.R.Q21*.

Lacerta schreiberi: CIPA 778*, 1256*, 1511*, 1517*; UAM.R.S-6*.

Lacerta trilineata: MDHC 240*, 241*, 295*, 356*.

Lacerta viridis: MNCN 16504*; NHMW 778*, 906*, 32879-3*.

Ophisops elegans: MDHC 281, 282; unnumbered specimen from the collection of Salvador Bailon.

Podarcis bocagei: UAM.R.PB48.

Podarcis filfolensis: MDHC 385.

Podarcis hispanicus: UAM.R.H30; two unnumbered specimens from the collection of Salvador Bailon.

Podarcis lilfordi: two unnumbered specimens from the collection of Salvador Bailon.

Podarcis melisellensis: MDHC 217, 218.

Podarcis muralis: MDHC 6, 65, 66, 72, 81, 89, 90, 222, 267, 311*, 312*, 313, 395, 413; MNHN 1992.192.

Podarcis siculus: MDHC 25, 91, 125, 229.

Podarcis tauricus: MDHC 244.

Podarcis tiliguerta: MDHC 153, 154.

Podarcis waglerianus: MDHC 390; MNHN 1992.189, 1992.190.

Psammodromus algirus: MNHN 1992.41; NHMW 788*; UAM.R.Ps9.

Timon lepidus: MDHC 216*; MNHN 1988.6629, 1991.4010, 1991.4242; unnumbered specimen stored in the Institut Català de Paleontologia Miquel Crusafont.

Zootoca vivipara: MDHC 179; UAM.R.Lv24.

Ablepharus kitaibelii: MDHC 239.

Chalcides bedriagai: unnumbered specimen from the collection of Salvador Bailon.

Chalcides chalcides: MDHC 94, 329, 398, 408.

Chalcides ocellatus: MDHC 193, 250; MNHN 1992.193; specimen number 28 from the collection of Salvador Bailon.

Chalcides striatus: MDHC 404; MNCN 16508; unnumbered specimen from the collection of Salvador Bailon.

Trachylepis aurata: MDHC 280; MNHN 1887-863.

Anguis gr. A. fragilis: MDHC 45, 49, 67, 102, 213, 221, 236, 237, 310, 367, 402.

Pseudopus apodus: MDHC 214, 215; MNHN 1918.95, 1992.199; PIMUZ A/III0975.

Blanus cinereus: MDHC 156; ZSM 175-1993-1, 175-1993-2, 227-1975, 548-2003, 652-0-1, 652-0-2, 653-0-1, 653-0-2.

Blanus mariae: ZSM 27-1988-1, 27-1988-2.

Blanus strauchi: MCCI R-1635, 1668; MDHC 93, 286, 287, 288.

Supplementary text S2

List of the published works dealing with the osteology of extant European lizards and worm lizards. The references marked with an asterisk provided useful information for the creation of the phylogenetic matrix.

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